The Distribution and Ecology of Sub-Littoral Species of *Macoma* (Bivalvia) off Moresby Island and in Satellite Channel, near Victoria, British Columbia

BY

R. M. DUNNILL

AND

D. V. ELLIS

Department of Biology, University of Victoria, Victoria, British Columbia, Canada

(9 Text figures; 3 Tables)

INTRODUCTION

THE GENUS *Macoma* LEACH, 1819 (Bivalvia) is widely distributed in northern seas and is also known to occur south of the equator in East Africa (THORSON, 1957, p. 106). It has undergone wide speciation, particularly in the eastern North Pacific and DUNNILL & ELLIS (1969) have confirmed 13 species presently occurring in the shallow coastal waters of southern British Columbia. Previous ecological studies (and incidental mention) of *Macoma* in the eastern North Pacific have in general been confined to the littoral species *M. inquinata* (DESHAYES, 1854), *M. nasuta* (CONRAD, 1837), *M. secta* (CONRAD, 1837), (amongst others, SHELFORD & TOWLER, 1925; SHELFORD *et al.*, 1935; MACGINITIE, 1935; ADDICOTT, 1952). The dearth of detailed ecological studies on sub-littoral species of *Macoma* probably stems from earlier confusion over the taxonomy of the genus.

This paper discusses the distribution of 8 species of *Macoma* occurring sub-littorally in an area of predominantly sandy sediments off the north end of Moresby Island, near Victoria, British Columbia, and examines the effects of some environmental factors.

Data from a previous benthic survey in adjacent Satellite Channel by ELLIS (1967 and in press) are included since this extends the range of sediment types covered.

[1] Based on part of a thesis submitted by R. M. Dunnill in partial fulfillment of the requirements for the degree of M. Sc. at the University of Victoria

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DESCRIPTION OF THE STUDY AREA

PHYSIOGRAPHY

Satellite Channel, on the south-western fringe of the Strait of Georgia, southern British Columbia (Figures 1 and 2) is roughly 13 nautical miles long, 1.5 to 2.0 nautical miles wide and has a mean depth of 73 m, although in several places, narrow elongated zones occur with depths greater than 90 m. Oceanic water has access to Satellite Channel from Swanson Channel and Haro Strait over a sill at a depth of 66 m.

Moresby Island lies at the east end of Satellite Channel at its junction with Swanson Channel.

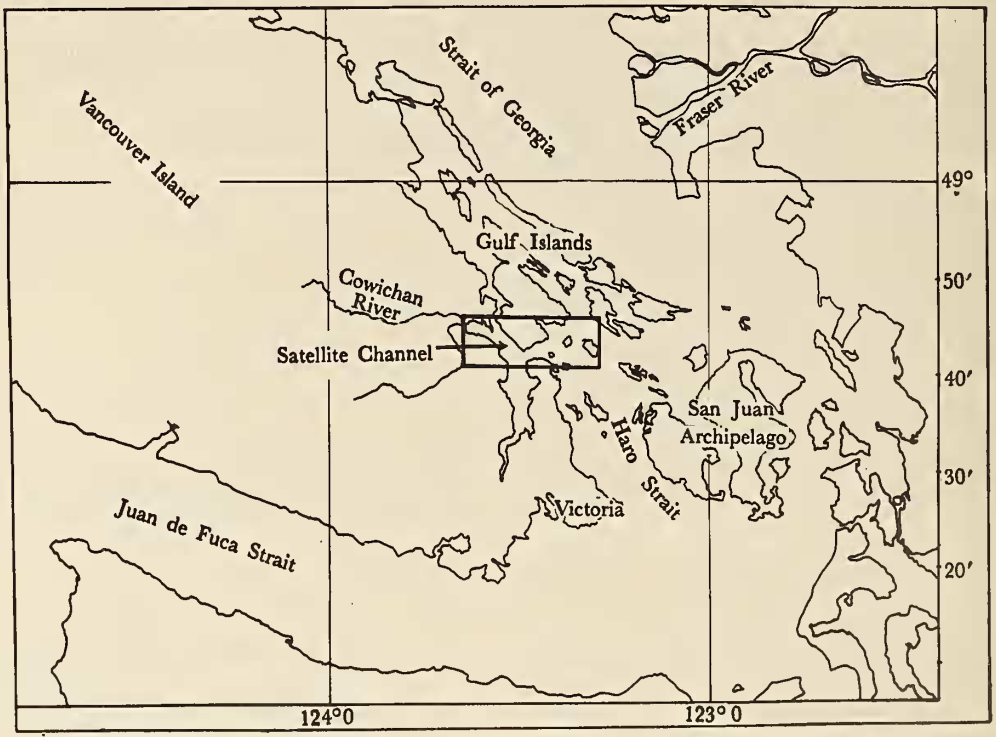

Figure 1

Satellite Channel in relation to southernmost British Columbia

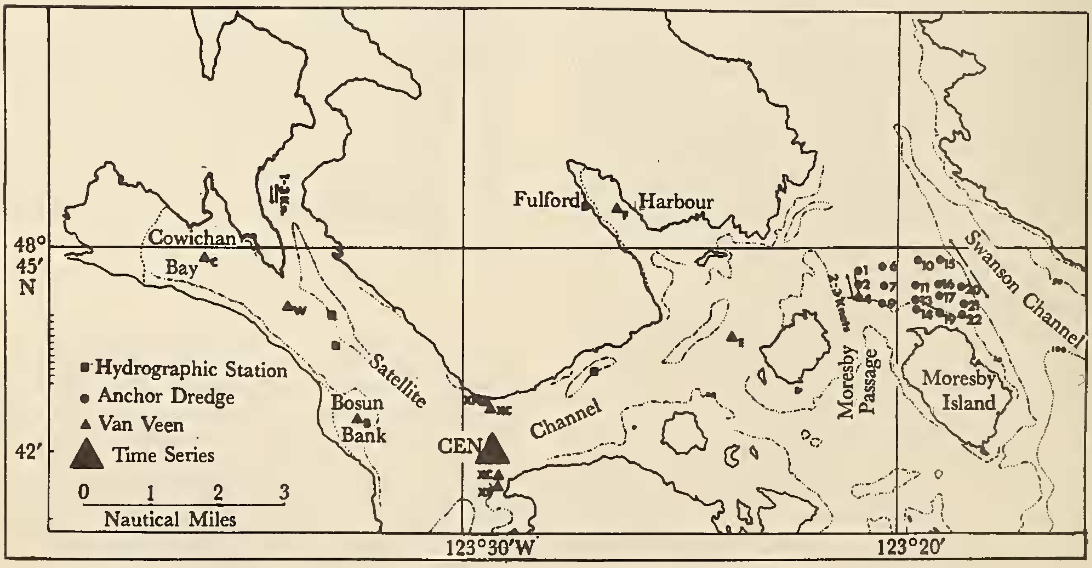

Figure 2

Satellite Channel and Moresby Island showing station localities

HYDROGRAPHY

Tully & Dodimead (1957) and Waldichuk (1957) discuss the oceanography of the Strait of Georgia.

According to Waldichuk (*op. cit.*), there are basically 3 water masses in the Strait of Georgia-San Juan system:

1. the brackish surface water from run-off in the Strait of Georgia (mainly from the Fraser River);
2. the deep water of oceanic origin in Juan de Fuca Strait; and
3. a mixture of (1) and (2) which forms at the sills between the straits.

Tidal currents in the southern region of Georgia Strait flow rapidly and turbulently in narrow passages between mazes of islands (Tully & Dodimead, 1957). Intensive tidal action, aided by wind and waves, particularly in winter, mixes the brackish surface layer with underlying more saline water to near homogeneity. Temperature and salinity stratification is minimal in the channels of the southern Strait.

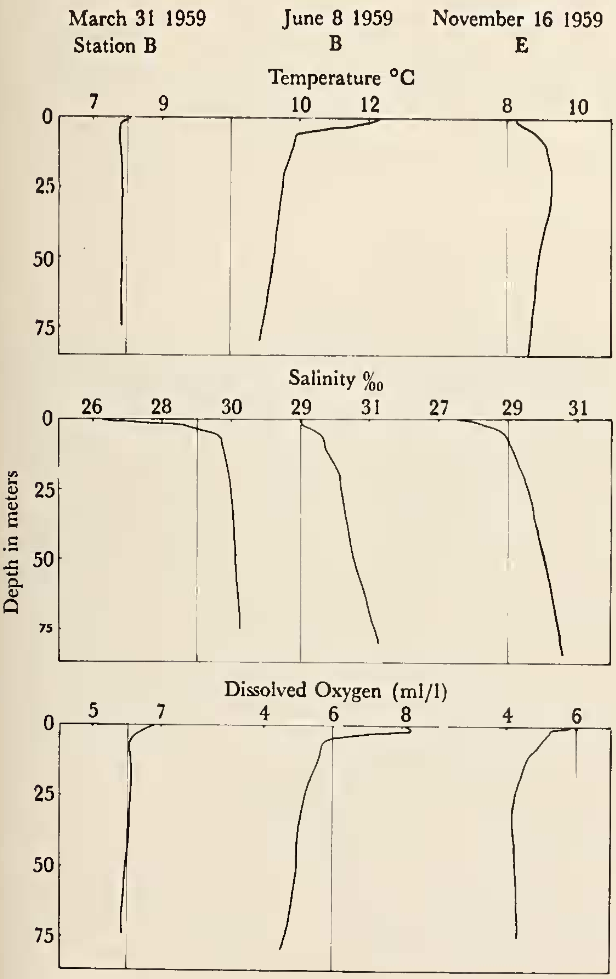

Figure 3

Water properties in Satellite Channel

In Satellite Channel, in the northwestern portion of the southern region, current velocities are lower, there is less mixing and more stratification develops. Seasonal changes in properties of the upper 75 - 80 m of the water column in Satellite Channel are shown in Figure 3, based on data from Herlinveaux *et al.* (1960) and Pacific Oceanographic Group (1959a and 1959b).

A pronounced thermocline, established in summer, is destroyed by increased mixing in winter. The deeper water averages about one degree Centigrade lower in winter than in summer.

Salinity changes mainly reflect the seasonal cycles of run-off of the Cowichan River (Herlinveaux, 1962). A prominent halocline develops in the upper 10 m in winter and spring, coinciding with maximal annual precipitation and run-off in the area at sea level. The surface lower salinity layer is much less in evidence in summer, when discharge from the Cowichan River is low. However, a less pronounced halocline persists, possibly indicating the presence of Fraser River outflow, which is maximal in summer.

From 15 - 85 m, temperature, salinity, and dissolved oxygen values show little seasonal or vertical variation. Temperatures range from 7.87 - 9.70° C, salinities from 29.25 - 31.46‰ and dissolved oxygen concentrations from 4.37 - 6.13 ml/l. Ranges in these properties seem too small for them to be important in limiting distribution of sub-littoral *Macoma* species in Satellite Channel at depths investigated. Water off the north end of Moresby Island, closer to regions of intense mixing than the hydrographic stations in Satellite Channel, probably is less stratified and has smaller ranges in temperature, salinity, and dissolved oxygen concentrations. Sediment temperatures measured off Moresby Island in the summer of 1967 (Table 1) had a range of less than 1° C at stations between 26.5 and 84.0 m.

GEOLOGY

Sediments in Satellite Channel and their Origins

There is a marked progression in the Satellite Channel trough from very fine grained sediments at the western end near the mouth of the Cowichan River to coarser grained sediments in the east (Figure 4). The mean silt-clay fraction was 95.4% in Cowichan Bay and 82.2% at the mouth of the bay. Further east, the silt-clay fraction had decreased to 40.3% at Satellite Channel Center and

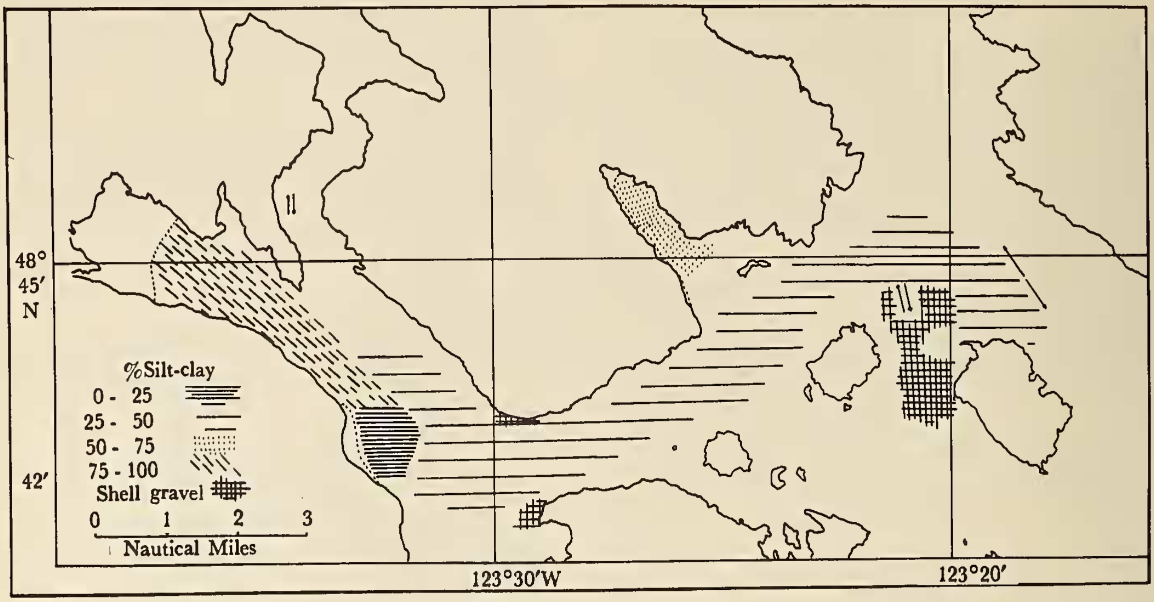

Figure 4

Generalized distribution of sediments in Satellite Channel

to 25.9% at Satellite Channel East. Excluding stations on "shell-gravels", the mean of the 13 stations (26 samples) on the finer sediments in the grid at the north end of Moresby Island was 31.3% silt-clay.

There were localized exceptions to this main trend. Bosun Bank on the west side of Satellite Channel, near its northwestern end, was noticeably sandy (15.3% silt-clay), while Fulford Harbour near the east end had fine grained sediments (69.2% silt-clay).

"Shell-gravels" occurred at 4 stations at the mouth of Moresby Passage (Figure 2), where currents reach 2 - 3 knots (Canadian Hydrographic Service, chart 3452).

The fine grained sediments at the west end of Satellite Channel, in the vicinity of Cowichan Bay, probably owe their origin to material carried down in suspension by the Cowichan River. It is improbable that the coarser grained fractions of the sediments in the channel trough originate from material brought down by the Cowichan River since these would, in that case, be deposited before the fine grained material in Cowichan Bay.

The sandy-silts of Fulford Harbour probably result from deposition from small streams, notably Fulford Creek.

Wang (1955) indicates that away from large rivers, much of the sediment added to the inland waters is derived from the erosion of shoreline glacial till. Most of the eroded clay and silt fractions are carried out to sea by the currents, leaving bottom sediments consisting of boulders, gravel, and sand. According to Wennekens (1959), erosion of shoreline glacial deposits provides a considerable part of sediments in the San Juan Archipelago. This process is undoubtedly important in the formation of bottom sediments in the Satellite Channel area also. "Shell-gravel" from the Moresby Island grid contained an assortment of small rocks (cobbles) of igneous, sedimentary and metamorphic origin, varying in outline from sub-rounded to sub-angular. There was also a finer matrix containing a considerable proportion of shell fragments and some intact dead bivalves enclosing a dark clay. It seems probable that this poorly sorted sediment results from erosion of a glacial till, possibly *in situ,* by selective washing out of silt and clay, leaving behind a coarser fraction, too heavy to be transported.

In the lee of the north end of Moresby Island, there is an area relatively sheltered from the currents that sweep through Moresby Passage and Swanson Channel. The sediments here are predominantly sandy although the silt-clay fraction of 26 samples varies from 14 to 46%. The bathymetry of this locale suggests eddies may build up when tidal currents reach their peak in the adjacent passages, carrying in and depositing material from suspension in a haphazard fashion. The bottom of this sedimentary bank slopes down to the channel trough more slowly than the bottom in the exposed areas of Swanson Channel, to the east. Dense bivalve populations, including large adults, whose growth rings show they are 8 or more years old, indicate the sediments of the bank are relatively stable.

METHODS

A grid of stations was established off the north end of Moresby Island and sampled in the summer of 1967. A 0.1 m^2 Van Veen grab, tried initially, would not work on "shell-gravels" and was replaced with a 52.0 l capacity anchor dredge, based on that in HOLME (1964). The anchor dredge was backed by a steel plate instead of a net, preventing "washing-out" of the sample, except at the bucket surface. Two samples were taken at each station and sample sizes ranged from 28.8 to 52.0 l (Table 1a, 1b). The dredge, when weighted as in Figure 5, was estimated to penetrate to a mean depth of 7.5 cm. Since sample volumes were known, approximate sample areas could be estimated.

In the Satellite Channel survey, 10 to 16 samples were taken at each station using 0.1 and 0.2 m^2 Van Veen grabs (Table 1c).

Figure 5

The weighted anchor dredge

Sediment samples were taken for particle analysis by a modification of the hydrometer technique of BOUYOUCOS (1951) and data are recorded in Table 1. After sample temperatures and volumes were measured, the entire samples were washed through a 2 mm square mesh wire screen and all macrobenthos picked out and preserved in 10% neutral formalin. *Macoma* count and weight data are recorded in DUNNILL (1968) and are shown graphically in Figures 6 and 7.

The "average size" of a population of a given species (the ratio of wet weight to number of individuals per meter squared), assuming the full size range of the species at that locality is sampled, is of some value as an indicator of environmental suitability. Where "average size" is relatively high for a species, the environment must be sufficiently favourable to allow continued survival of individuals to a (relatively) large size. Where "average sizes" at a given locality are very small, first impressions are that environmental conditions there are unfavourable to the species, which is either failing to survive to a large size (i. e., is very short lived) or has a very slow growth rate. However, the investigator might be sampling a young population in a favourable environment. Counting growth rings would show the actual age of the population. A second sampling of a young population after the lapse of a year or two would indicate whether or not that population of the species was surviving and environmental conditions were favourable.

Successful migration of adult specimens of *Macoma* over any appreciable distance would seem unlikely, at least in Satellite Channel, since the area supports considerable numbers of bottom fish.

RESULTS

Macoma in Relation to the Physical Environment

Eight species of *Macoma* were found sub-littorally on the Moresby Island grid and two additional species, *M. inquinata* and *M. nasuta,* were found intertidally at the north end of the island. Thus at least 10 of the 13 species found in southern British Columbia (DUNNILL & ELLIS, 1969) occur within a very small area at the north end of Moresby Island.

Macoma inquinata and *M. nasuta* are both shallow water species in the study area and were not found in grab or dredge samples either off Moresby Island or in Satellite Channel. They will not be considered further in this study.

Macoma yoldiformis CARPENTER, 1864 was found at a single location, station 19 (29 m, 25.0% silt-clay). Accordding to BERNARD (1967), the species ranges from intertidal to 18 m in British Columbia. It was found in Sooke

Table 1

Station List, Sample Sizes, Sample Areas
and Environmental Data

(a) Moresby Island grid - excluding stations on "shell-gravel"

Station	Depth (m)	Sample Volume (l)	Estimated area sampled (m²)	Sediment Temp. (°C)	% silt-clay
1	80	52.0	0.69	–	38.0
6	65	52.0	0.69	–	23.0
10	73.5	45.6	0.60	–	41.5
11	55.5	46.5	0.62	9.8	14.0
13	35.5	37.5	0.50	9.9	29.0
14	26.5	41.1	0.55	10.1	32.0
15	77.5	52.0	0.69	–	39.5
16	62.5	44.8	0.60	9.5	32.0
17	53.5	40.2	0.54	9.6	36.0
19	29.0	52.0	0.69	9.9	25.0
20	85.0	52.0	0.69	–	22.5
21	84.0	44.8	0.60	9.4	32.0
22	74.0	44.8	0.60	9.9	45.5

(b) Moresby Island grid - stations on "shell-gravel"

Station	Depth (m)	Sample Volume (l)	Estimated area sampled (m²)	Sediment Temp. (°C)	% silt-clay
2	55.0	49.2	0.65	10.0	42.0[1]
4	33.5	34.9	0.46	–	34.5[1]
7	53.5	52.0	0.69	9.5	43.0[1]
9	40.5	44.7	0.59	9.8	37.5[1]

[1] % silt-elay in sediment fraction passing a 2 mm screen

(c) Satellite Channel

Station		Depth (m)	Sample Volume (l)	Sediment Temp. (°C)	Bottom Salinity (‰)	% silt-clay
F	(Fulford Harbour)	22.7	33.9[1]	–	–	69.2
CEN	(Satellite Channel Center)	74.5	10.0	8.3-9.2	29.40-32.48	40.4
XS	(Cross Section South)	9.0	5.3	–	–	9.5
XN	(Cross Section North)	9.0	1.3	–	–	10.8
B	(Bosun Bank)	14.9	3.1	7.4	29.90	15.3
C	(Cowichan Bay)	61.0	12.0	8.1	29.99	95.4
W	(Satellite Channel West)	68.9	10.9	8.1	29.77	82.2
E	(Satellite Channel East)	50.5	5.9	7.9	30.03	25.7

[1] benthos sampled with a 0.2 m² Van Veen grab (all other stations sampled with 0.1 m² grab)

Basin, near Victoria (DUNNILL & ELLIS, 1969) at 22 m in a black silt (78.9% silt-clay), hence is tolerant of a considerable range of sediment grain sizes. Probably most of the stations sampled off Moresby Island and in Satellite Channel were below the bathymetric range of *M. yoldiformis* in southern British Columbia.

Both station 19, in the lee of Moresby Island, and Sooke Basin are in sheltered locations. The species also occurs in a protected situation in Nanoose Bay, Vancouver Island. Shelter from strong currents appears to be a prerequisite for this small, fragile species to become established.

Despite the wide variation in sediment types found in the survey areas (see section on Geology), few clear-cut differences were found in the distribution of the remaining 7 species, *Macoma alaskana, M. brota, M. calcarea, M. carlottensis, M. elimata, M. incongrua,* and *M. lipara.* Often many of these species occurred together (Figures 6 and 7) at the same station. All are sub-littoral, with bathymetric ranges in southern British Columbia extending below the deepest station sampled. Ranges of these species are listed in Table 2 and bathymetric distribution trends shown in Table 3.

Macoma alaskana DALL, 1900 was somewhat restricted in its distribution. Where it was found, "average sizes" of individuals tended to be greatest at the deeper stations, below about 50 m, although the greatest density was at a shallow station (no. 19, 29 m).

Like *Macoma carlottensis, M. alaskana* was present at some stations and absent at others where depths and sediments were almost identical, indicating some other factor was limiting. It was not found at the more exposed stations adjacent to Swanson Channel (Figure 2) where currents might be too strong for small species such as *M. alaskana* to become established, nor was it found in the very fine-grained sediments in Cowichan Bay and Fulford Harbour (Figure 4).

Macoma brota DALL, 1916 was widely distributed in the survey areas, with a trend for greatest biomasses and "average sizes" of individuals to be found at depths of more than 40 m. Densities, biomasses and "average sizes" were generally greater off Moresby Island and at Satellite Channel East than elsewhere in Satellite Channel. "Average sizes" of *M. brota* on very fine-grained sediments were relatively low in comparison with those off Moresby Island, yet would still seem too high for it to be said that these sediments were unfavourable to the species.

Macoma calcarea (GMELIN, 1791) was present in collections from most stations off Moresby Island, but was not found elsewhere in Satellite Channel, although it is known to occur a few miles north of Cowichan Bay. Densities, biomasses, and "average sizes" all were markedly greater in water deeper than about 40 m.

The apparent absence of *Macoma calcarea* in areas where sediments were very fine-grained, i. e., Fulford Harbour and Cowichan Bay, suggest grain size may be an important limiting factor for the species. Possibly the sheltered conditions in some of these localities, reflected by fine bottom sediments, or even the annual deposition of fine-grained material from winter run-off of the Cowichan River, may also be unfavourable.

Macoma carlottensis WHITEAVES, 1880 was widely distributed in the survey area and showed no obvious preference for any particular depth zone or sediment grade. Densities and biomasses were roughly equally great at extremes of depth and sediment types surveyed, but "average sizes" tended to be low on the coarse and fine sediment extremes.

The species was found in equally high densities in sheltered environments in Fulford Harbour and Cowichan Bay and in more exposed conditions at Satellite Channel East and West.

Macoma elimata DUNNILL & COAN, 1968, the most widely distributed *Macoma* in the survey area, was found in greatest densities at shallow stations (less than 40 m), but biomasses and "average sizes" tended to be greatest in water deeper than 40 - 50 m.

Very fine sediments, as in Cowichan Bay and at Satellite Channel West, appear unfavourable to the species. Biomasses and "average sizes" there were low, even in water deeper than 50 m. However, the species was present in fine sediments in Fulford Harbour with relatively high density, biomass, and "average weight." The species apparently has a tolerance for a fairly wide range of sediment types.

Macoma incongrua (VON MARTENS, 1865) was the only *Macoma* regularly found on "shell-gravels," at stations exposed to strong currents (2 - 3 knots) sweeping through Moresby Passage. However, the greatest "average sizes" of individuals of the species were found at stations away from the "shell-gravels" where current velocities were lower (1 - 2 knots).

At the mouth of Moresby Passage (Figure 2), a reef with an average depth of about 36 m (and exposed at one point as Canoe Rock) affords stations below this depth some protection from currents. Densities, biomasses, and "average sizes" of the species on the "shell-gravels" here increased as depth and degree of shelter increased. At all stations surveyed, densities, biomasses, and "average sizes" of individuals tended to be greatest in water deeper than 40 - 50 m.

Macoma incongrua was generally not found at stations where sediment contained more than about 50% silt-clay

Table 2

Ranges in Distribution of *Macoma* off Moresby Island and in Satellite Channel

Species	Depth Range where found (m)	% silt-clay where found	Maximum Density (/m²)	Maximum Biomass (g/m²)	Range of "Average Sizes" (g)
Macoma alaskana	14.2-65.0	14.0-36.0	18.1	11.2	0.03- 1.2
Macoma brota	14.2-85.0	15.3-95.4	52.2	449.0	0.03-12.0
Macoma calcarea	29.0-85.0	14.0-45.5	225.0	873.0	0.7 - 7.4
Macoma carlottensis	9.0-80.0	9.5-95.4	344.0	13.6	0.01- 0.25
Macoma elimata	9.0-85.0	9.5-95.4	157.0	117.0	0.13- 3.0
Macoma incongrua	9.0-85.0	9.5-82.2	89.2	182.1	0.02- 4.3
Macoma lipara	29.0-85.0	14.0-45.5	17.0	392.0	6.4-42.9

[data from DUNNILL, 1968]

and where it did occur in such sediments, densities, biomasses, and "average sizes" were low.

Macoma lipara DALL, 1916 was collected at every station off Moresby Island, but elsewhere was found only at Satellite Channel East. There was a trend for densities, biomasses, and "average sizes" to be greatest at depths of more than 40 m. "Average sizes" were generally high, even for this, the largest sub-littoral *Macoma* species in southern British Columbia and indicate a scarcity of young individuals. Possibly the species may have had poor

Table 3

Trends in Distribution of *Macoma* off Moresby Island and in Satellite Channel

Species	Maximum Densities	Maximum Biomasses	Maximum "Average Sizes"
Macoma alaskana	Generally shallower than 50 meters	Generally shallower than 50 meters	Deeper than 40 meters
Macoma brota	Generally deeper than 40 meters	Generally deeper than 40 meters	Deeper than 40 meters
Macoma calcarea	Generally deeper than 40 meters	Generally deeper than 40 meters	Deeper than 40 meters
Macoma carlottensis	Roughly equal at shallow and deep stations	Roughly equal at shallow and deep stations	Roughly equal at shallow and deep stations
Macoma elimata	Shallower than 50 meters	Roughly equal at shallow and deep stations	Deeper than 40 meters
Macoma incongrua	Roughly equal at shallow and deep stations	Roughly equal at shallow and deep stations	At the deeper stations
Macoma lipara	Generally deeper than 40 meters	Generally deeper than 40 meters	Deeper than 40 meters

success in reproducing itself in the last few years at the north end of Moresby Island.

The apparent absence of the species in sheltered locations and on fine-grained sediments indicates these are unfavourable to *Macoma lipara*. Large adult specimens were regularly found near the surface of the sediments, suggesting the species is a shallow burrower. However, PAMATMAT (1961) found distribution of *M. secta,* another large (intertidal) species independent of size, and this may also be true of *M. lipara*.

DISCUSSION

In shell morphology, *Macoma brota, M. calcarea, M. elimata,* and *M. lipara* are very similar and their similarity is apparently reflected in their environmental requirements. They are frequently found together off Moresby Island (Figures 6 and 7). Examination of Figure 8 shows these species all tend to have maximum biomasses and "average sizes" in water deeper than about 40 m and in sediments with a silt-clay content between roughly 15 and

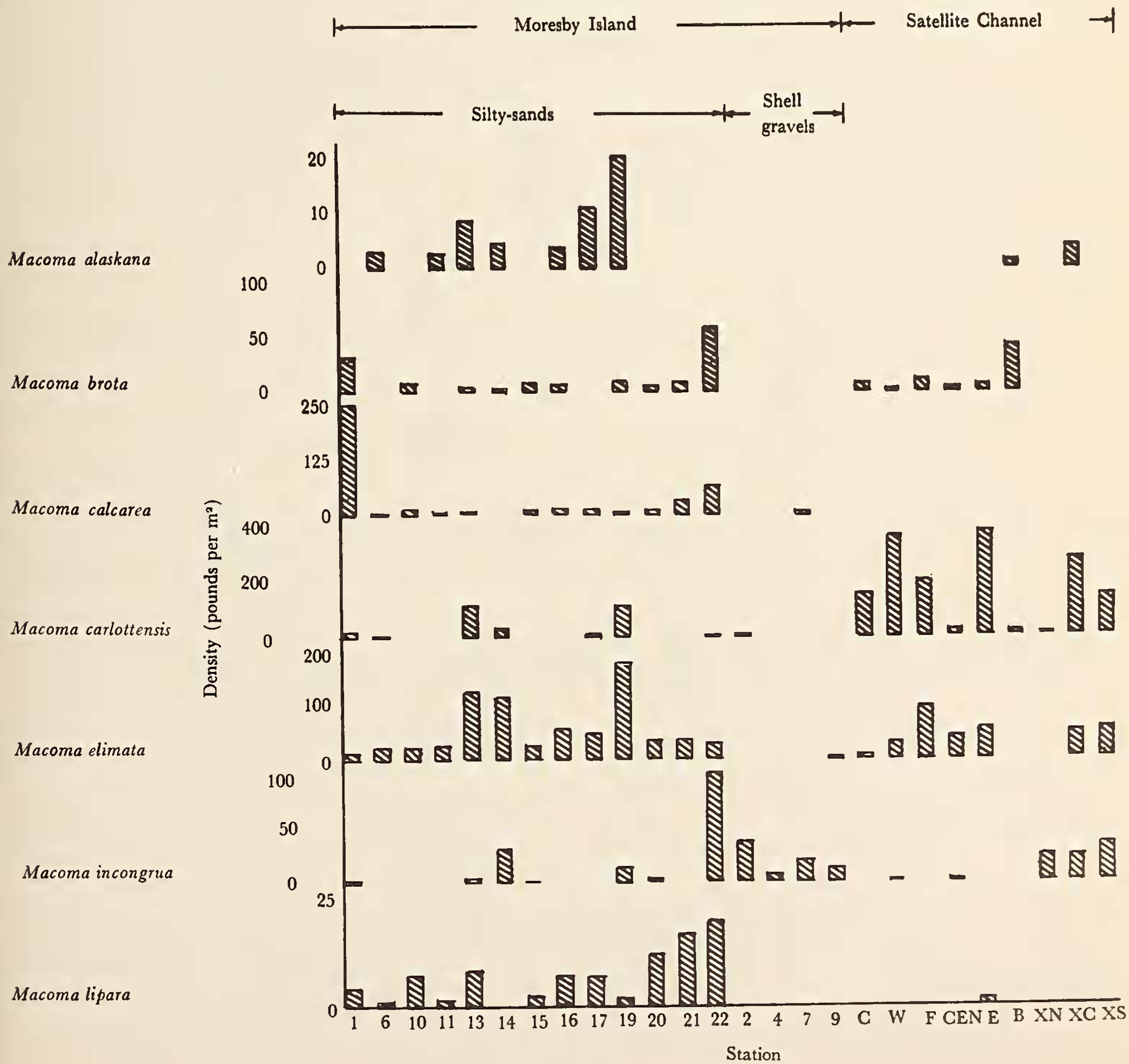

Figure 6

Densities of populations of sub-littoral species of *Macoma* off Moresby Island and in Satellite Channel

50%. *Macoma calcarea* and *M. lipara* are apparently more restricted in their distribution than *M. brota* and *M. elimata* and perhaps are less tolerant of the finer grained sediments.

The presence of *Macoma brota* and *M. elimata* on these very fine-grained sediments (containing more than 80% silt-clay) and the low "average size" of individuals, suggest the young of these animals are carried into unfavourable situations, settle there but are then short-lived and probably fail to survive to reproductive maturity, in which case they are dependent on replacement from outside populations in more favourable locations.

The smaller species, *Macoma alaskana* and *M. incongrua* (Figure 9) also appear to favour water deeper than 40 - 50 m and sandy sediments. *Macoma carlottensis* is exceptional and appears tolerant of shallower water and

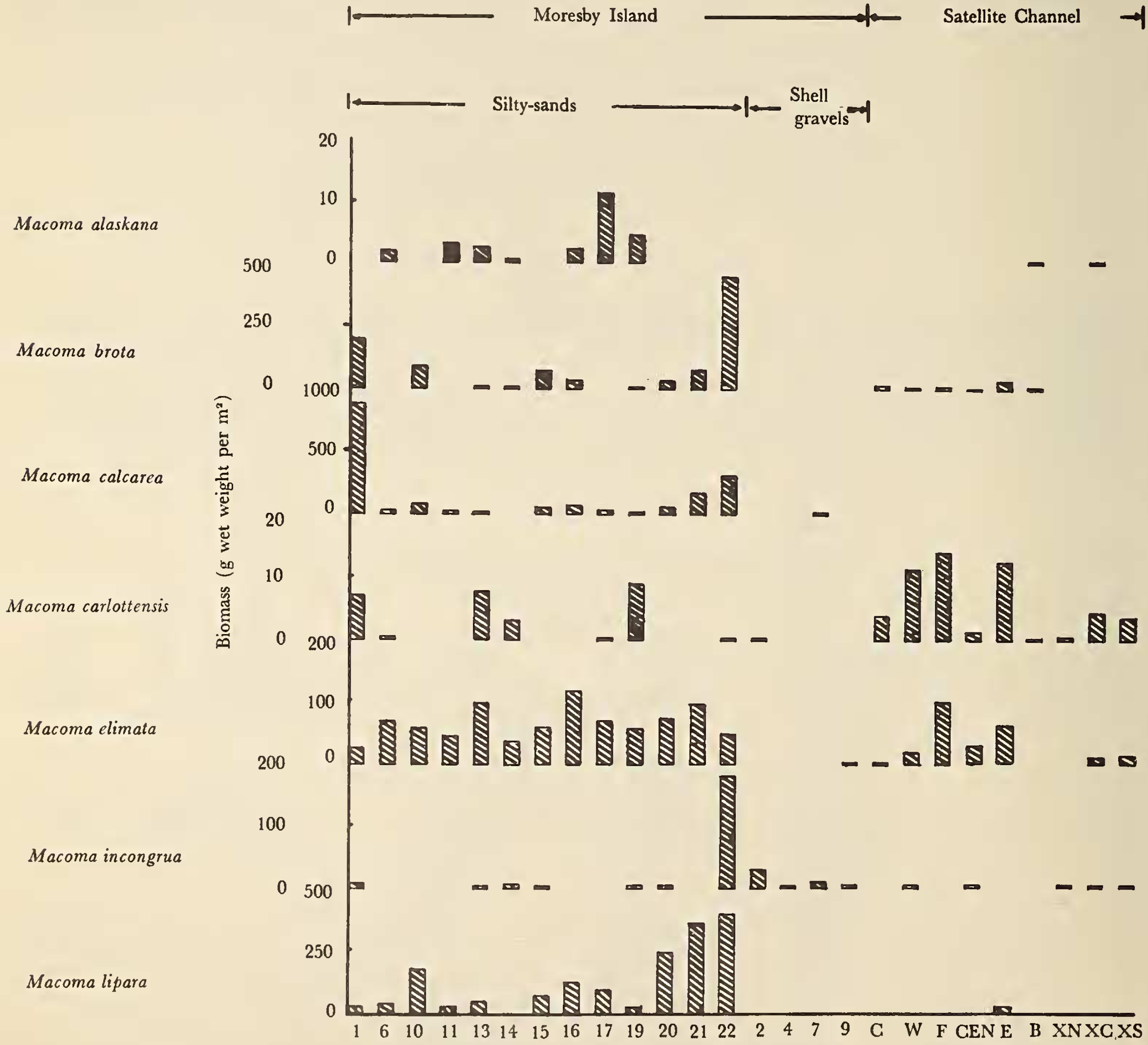

Figure 7

Biomasses of populations of sub-littoral species of *Macoma* off Moresby Island and in Satellite Channel

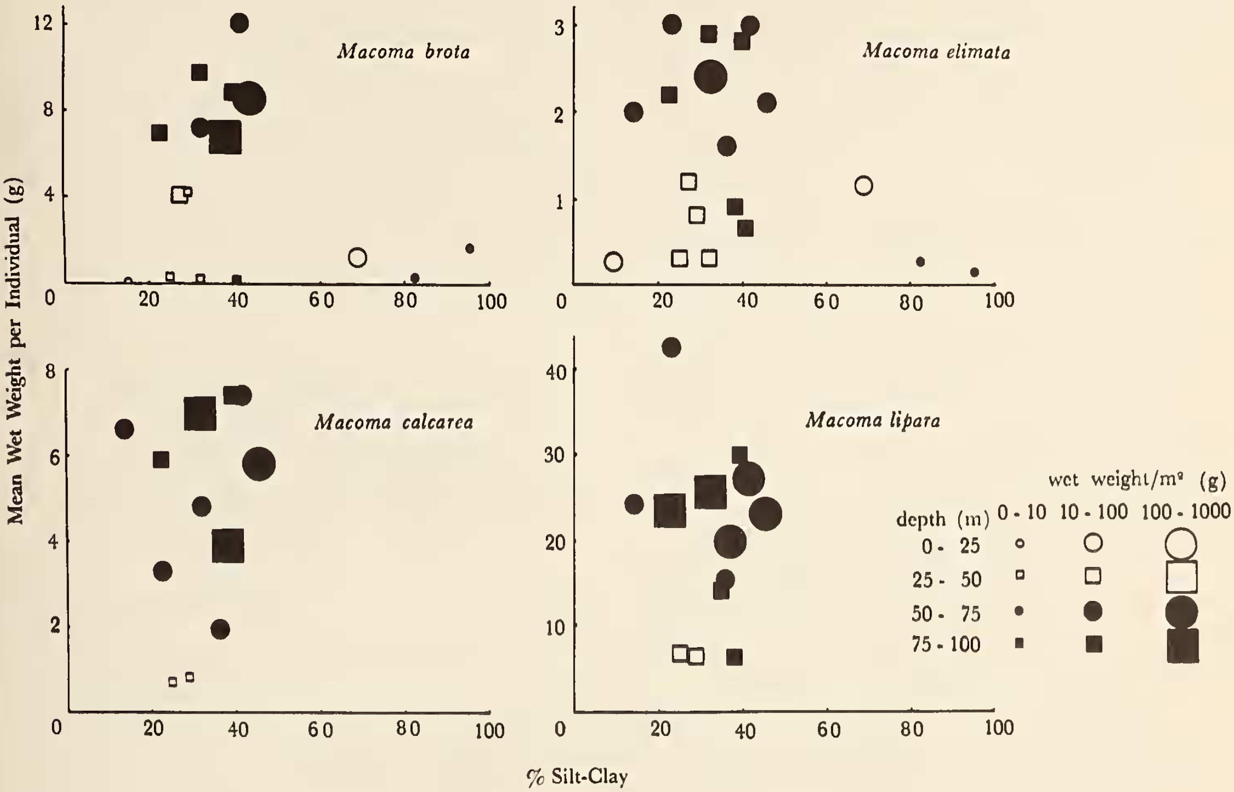

Figure 8

Plots of "average size" of *Macoma brota, Macoma calcarea, Macoma elimata* and *Macoma lipara* versus depth and % silt-clay in sediments

a greater range of sediment types than the other species examined.

The mean number of different species of *Macoma* occurring in hauls off the north end of Moresby Island on silty-sands was 5.3 compared to only 1.7 on "shell-gravel" (Figures 6 and 7). In the rest of Satellite Channel, the mean was 3.3. The paucity of *Macoma* species found on "shell-gravels" seems to result from the prevailing strong currents there which may prevent them from becoming established or may hinder their feeding. The siphons of species such as *Modiolus modiolus* (Linnaeus, 1758) and *Humilaria kennerleyi* (Reeve, 1863), which flourish on the "shell-gravels," are very short and have wide bores, in diametric contrast to those of *Macoma,* which are very long and of small bore. However, observations made on sub-littoral *Macoma* species in aquaria suggest some of these are not obligatory detrital feeders but can shorten their inhalant siphons and feed from the water above the bottom. This behaviour has also been reported for the Atlantic species, *Macoma balthica* (Linnaeus, 1758) (Braefield & Newell, 1961).

The mean wet weight/m² of all macomas taken with the 0.1 m² Van Veen grab from 8 stations below 40 m off the north end of Moresby Island, was 1737 g (= 114 g dry organic matter/m², using the mean of the conversion factors for *Macoma* listed in Thorson (1957)). It is evident that the area has an exceptionally rich infaunal standing crop. In comparison, Holme (1963) and Sanders (1956) obtained total faunal mean dry organic matter weights of 11.2 and 54.627 g/m² for the English Channel and Long Island Sound, respectively. Food must be plentiful off Moresby Island to support this large standing crop and may not at present be a limiting factor governing the densities and biomasses of *Macoma* in this location.

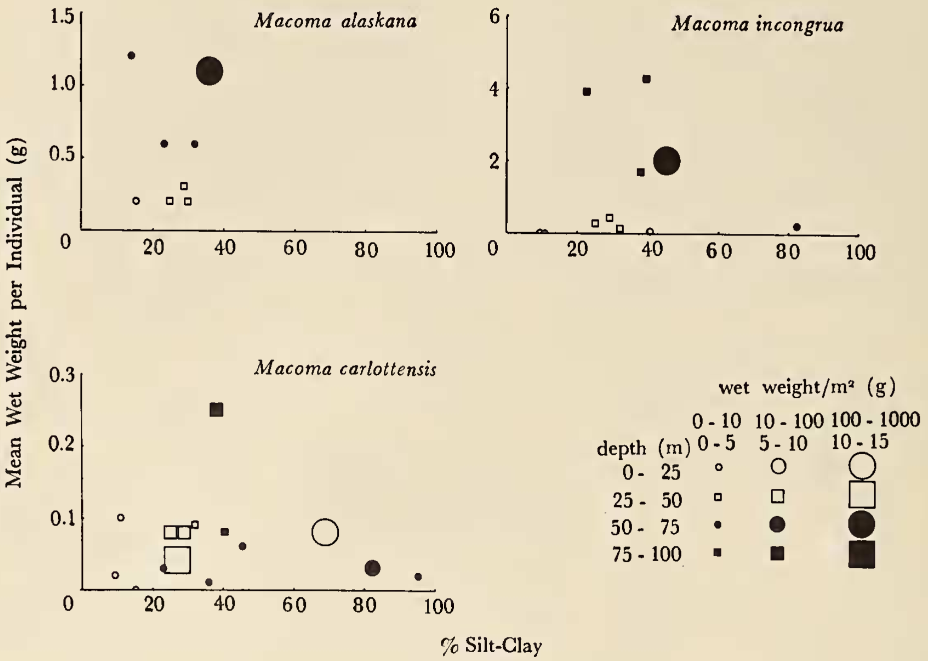

Figure 9

Plots of "average size" of *Macoma alaskana, Macoma carlottensis* and *Macoma incongrua* versus depth and % silt-clay in sediments

Frequently, 6 different species of *Macoma* were taken in a single anchor dredge haul at the north end of Moresby Island, from an estimated area of less than $0.7 m^2$, and 5 different species were taken from areas of $0.1 m^2$ with the Van Veen grab (see DUNNILL, 1968). At station 19, the two anchor dredge hauls captured between them all 8 species of *Macoma* found sub-littorally in the survey (Figures 6 and 7). *Macoma yoldiformis,* collected at station 19, is not figured since the authors consider it a littoral species.

According to GAUSE (1934), as a result of competition, two similar species scarcely ever occupy similar niches (by niche he means ". . . what place the given species occupies in a community, i. e. what are its habits, food and mode of life."), but displace each other so that each utilizes "certain peculiar kinds of food and modes of life in which it has an advantage over its competitor."

It seems probable that the merging and diverging of currents flowing through the channels at the north end of Moresby Island would generate extensive eddies. These might aid in dispersal of larvae of all local species over the submerged bank and could thus account for the different species being brought together initially. There is some evidence (see above) that food may be more than adequate to support the existing *Macoma* populations off Moresby Island so that interspecific competition is lessened, thus permitting the coexistence of these closely related species. However, determination of the exact "niches" occupied by each of these coexisting species of *Macoma* off Moresby Island is beyond the scope of the present study.

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